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THE VELIGER

The Anatomy and Systematics of *Ceratoxancus*, a Genus of Deep-Water Ptychatractinae (Gastropoda: Turbinellidae) with Labral Spine

by

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Abstract. The anatomy of *Ceratoxancus* is characterized by a short or very short proboscis, the presence of an accessory salivary gland, the ventral odontophoral retractor passing through the nerve ring, and the position of the buccal mass at the proboscis base in contracted condition. These characters are shared by other representatives of the subfamily and confirm the classification of *Ceratoxancus* in the Ptychatractinae, until now based on shell and radula characters. *Ceratoxancus* Kuroda, 1952, comprises six species of which four are described as new from the New Caledonia region in deep water (530–830 m). *Ceratoxancus elongatus* Sakurai, 1958, is removed from the synonymy of *C. teramachii* Kuroda, 1952, and both species are recorded from the southwest Pacific. Species of *Ceratoxancus* with a long labral spine present numerous shell breakages, while toothless species have much fewer scars, and it is hypothesized that the tooth and outer lip are used in prey capture with accompanying shell breakage.

INTRODUCTION

The genus *Ceratoxancus* was introduced for the single species *C. teramachii* Kuroda, 1952, from deep water off Japan, and was tentatively assigned to the family Turbinellidae on the basis of its radula (Kuroda, 1952). A second species, *C. elongatus* Sakurai, 1958, was subsequently synonymized (Habe, 1964) with *C. teramachii*. Outside of Japan, *Ceratoxancus* has been reported in the literature only once, from Hawaii (Cernohorsky, 1977), and the genus is currently known from the shells of the two nominal species and the original description of the radula and operculum of *C. teramachii*.

In the present paper, we describe the anatomy of five species of *Ceratoxancus*, including the type species, and briefly discuss the taxonomic position of the genus. We review its species-level systematics, based on new material from the southwest Pacific, and describe four new species. In forthcoming papers, we will describe the anatomy and revise the systematic contents of other genera of deep-water Turbinellidae, based on new, rich material from recent expeditions of the Muséum National d'Histoire Naturelle, Paris (MNHN). All material cited, unless otherwise stated, is stored in MNHN.

Abbreviations and text conventions: ag, anal gland; asg, accessory salivary gland; cme, cut mantle edge; ct, ctenidium; dd, dead collected specimen; dg, digestive gland; gL, gland of Leiblein; lv, live collected specimen; ml, mantle lobe; moe, glandular mid-esophagus; ne, nephridium; ng, nephridial gland; nr, nervous ring; od, odontophore; oe, esophagus; op, operculum; os, osphradium; p, penis; ped.n, pedal nerves; poe, posterior esophagus; pr, proboscis; prp, proboscis protractors; prs, rhynchodaeum (= proboscis sheath); s, siphon; sem.gr, open seminal groove; sem.p, seminal papilla; sg, salivary gland; st, stomach; t, head tentacle; tes, testiculus; vL, valve of Leiblein; vodr, ventral

odontophoral retractor; vprr, ventral proboscis retractor.

Repositories: AMNH, American Museum of Natural History, New York; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington.

ANATOMY

The anatomy of the five species dissected is very similar. Therefore, it is described in full for the type-species *Ceratoxancus teramachii* and for *C.* ***basileus*** sp. nov., which is conchologically less similar to its congeners. Only major differences are mentioned for the other two species. Upon collection, material of *Ceratoxancus elongatus, C.* ***niveus*** sp. nov., and *C.* ***basileus*** sp. nov. had been dumped into alcohol, while material of *C. teramachii* and *C.* ***melichrous*** sp. nov. had been preserved in buffered formalin.

Ceratoxancus teramachii

The largest specimen (New Caledonia, MUSORSTOM 5, sta. DW337) was dissected. It has a shell length of 31.5 mm, last teleoconch whorl length 21.5 mm, aperture length 14.0 mm, siphonal canal length 3.6 mm, shell diameter 12.6 mm. A specimen sectioned (MUSORSTOM 5, sta. DW338) has a shell length of 14.9 mm, last teleoconch whorl length 10.9 mm, aperture length 6.6 mm, shell diameter 7.4 mm.

External anatomy (Figure 1A, B): The body consists of 3.75 whorls; the mantle spans one whorl, the nephridium 0.3 whorl, and the digestive gland 1.25 whorl. The body is pale yellowish. The operculum is medium-sized, occupying at least 0.4× aperture length (lower part of the operculum with nucleus damaged), elongate leaf-shaped and recurved, thin, transparent, and yellow (Figure 1C). The columellar muscle is attached in the upper third of the operculum. The foot is short (L/W ≈ 1.5). The siphon is short, simple, pale greyish. The columellar muscle is very thick with three deep grooves corresponding to the columellar teeth. The mantle is thin, the mantle organs clearly visible through it. Near the siphon, the mantle has a rounded lobe with a longitudinal groove in the middle. This lobe forms the labral spine. The head is broad with short, stout tentacles and large eyes. The border between mantle cavity and the nephridium is represented by a deep cleft.

Mantle: The ctenidium is very long and occupies 0.75× mantle length, narrow (L/W ≈ 7.5), with high hanging leaflets. The osphradium is large, 0.75× as long and 1.5× as wide as the ctenidium, asymmetrical with the right side nearly twice as broad as the left. The hypobranchial gland is covered with a thick mucus layer and is not transversely pleated. The anal gland is seen through the mantle as a narrow dark strip.

Digestive system: The organs of the body haemocoel are compact (Figure 1D). The proboscis in the contracted state is very short (about 2 mm), smooth, and occupies only about half of the rhynchodeal cavity. The rhynchodaeum (= proboscis sheath) is thick-walled and lined with a tall epithelium. The very powerful paired muscles, probably functioning as ventral proboscis retractors, are attached latero-ventrally to the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel. This probably indicates that the whole rhynchodaeum takes part in proboscis evertion, and when the proboscis is completely everted, these retractors are attached to the inner wall of the proboscis. Apart from the major retractors, there are a few smaller retractors attached to the rhynchodaeum laterally, and posteriorly to the anterior ventral retractor.

The buccal cavity is lined with a thick cuticular layer. The buccal mass is long and muscular, and projects beyond the rear of the retracted proboscis. In longitudinal sections the radular diverticulum is seen to open into the buccal cavity at the proboscis base in its contracted state. The odontophoral subradular cartilages are paired, not fused anteriorly. The large, paired ventral odontophoral retractors pass through the nerve ring, follow the bottom of the cephalic haemocoel, and join the columellar muscle.

The radula (Figure 2A–D) is about 3.8 mm long (12% of shell length and 27% of aperture length) and about 165 μm broad (0.52% of shell height and 1.17% of aperture length); it projects beyond the rear of the proboscis, and consists of about 180 transverse rows. The rachidian teeth are very closely spaced (Figure 2B), thus preventing the examination of the shape of the basal part. They bear three sharp cusps, emanating from the posterior edge of the basal part. The central cusp is nearly twice as long as the lateral ones. The lateral teeth are unicuspid, with a long, narrow base (Figure 2C). The length of the lateral tooth base equals 0.66× the rachidian width.

After leaving the proboscis, the esophagus forms a short loop before opening into the valve of Leiblein (Figure 1E). Between the valve and the opening of the gland of Leiblein, the esophagus is rather widened and apparently glandular. This part, representing the mid-esophagus, is long and

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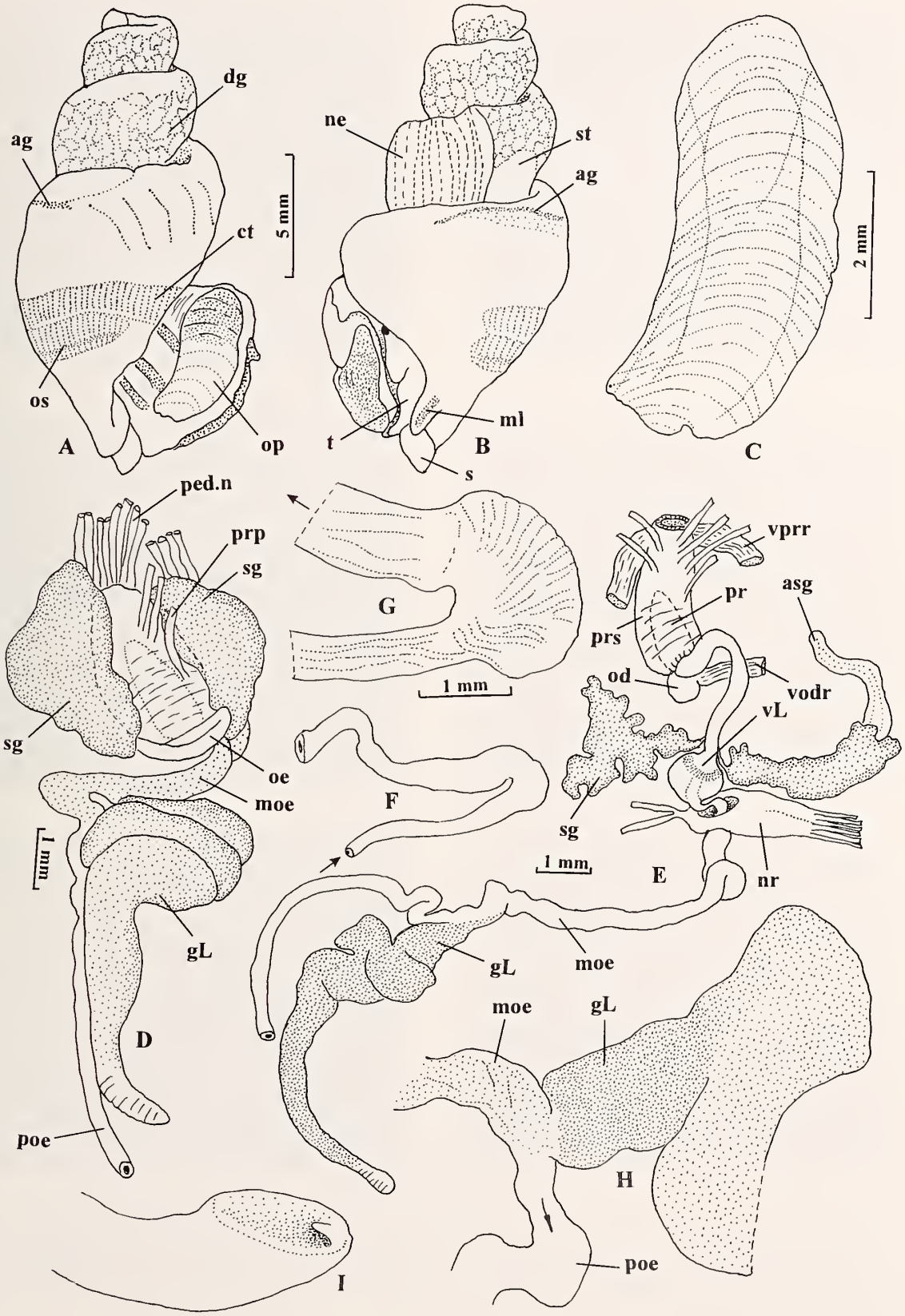
Figure 1

Anatomy of *Ceratoxancus teramachii*. A–H, female (MUSORSTOM 5, sta. DW337, shell height 31.5 mm). I, male (MUSORSTOM 5, sta. DW338, shell height 14.9 mm). A, B, body, removed from the shell; C, operculum; D, organs of the body haemocoel in natural position; E, organs of the body haemocoel, expanded; F, outer view of the stomach in the same scale as E; G, outer view of the stomach; H, opening of the gland of Leiblein into mid-esophagus, from the ventral side; I, tip of the penis.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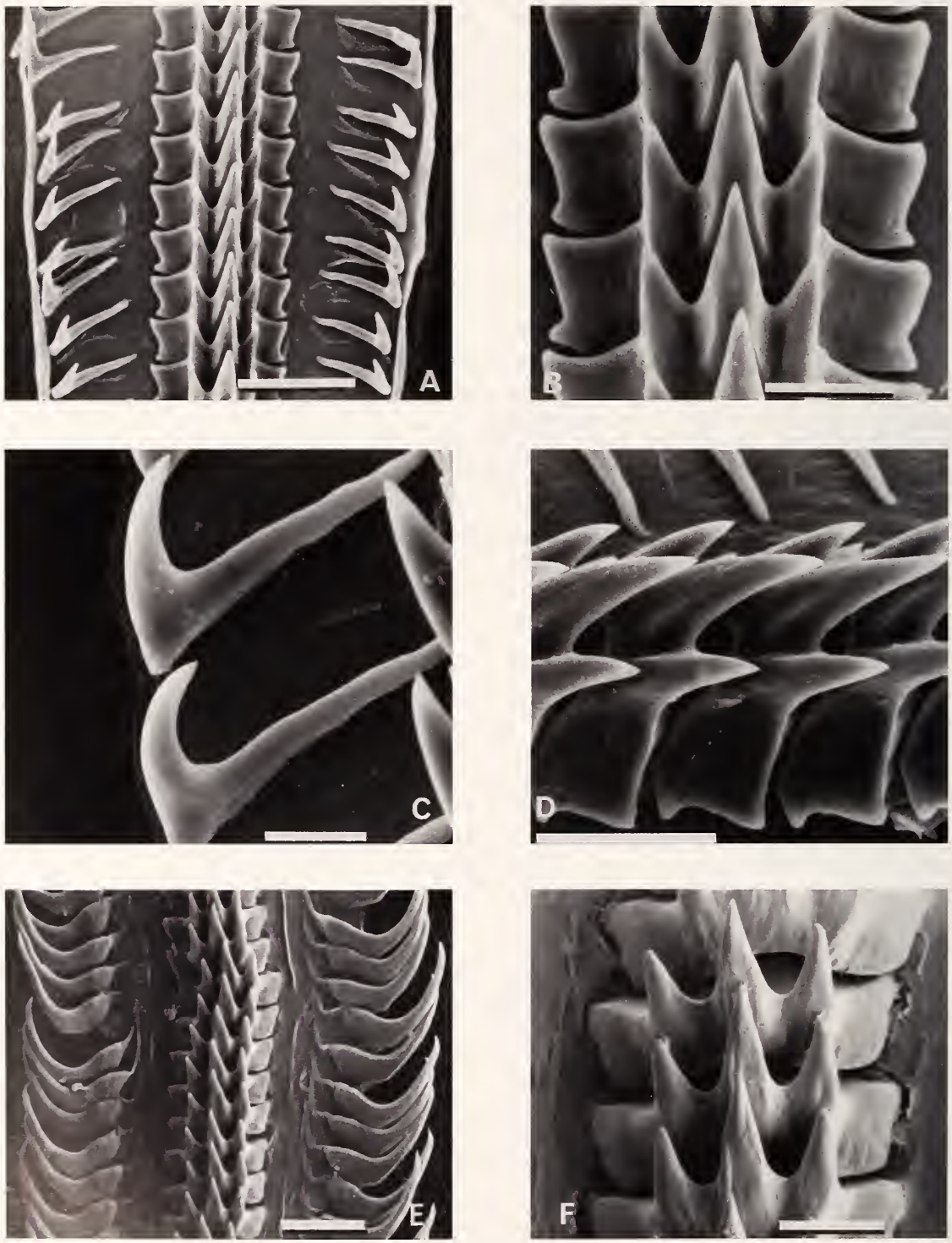


Figure 2

Radulae of *Ceratoxancus* spp. *Ceratoxancus teramachii* (A–D) (MUSORSTOM 5, sta. DW337): A, dorsal view of the radular ribbon; B, enlarged rachidian teeth; C, enlarged lateral teeth; D, lateral view of rachidian teeth. *Ceratoxancus* ***melichrous*** Kantor & Bouchet, sp. nov. (E, F) (BATHUS 3, sta. DW 776): E, dorsal view of the radular ribbon; F, enlarged rachidian teeth. Scale bars 50 μm (A, E); 20 μm (B, D, E); 10 μm (C).

convoluted. When the organs of the haemocoel are stretched by dissection, the glands lie on both sides of the valve of Leiblein, which is well defined, much broader than the esophagus, and pyriform, with a conical ciliary valve. The posterior esophagus runs along the left side of the gland of Leiblein and opens into the stomach.

The stomach is very small by comparison to the anterior foregut, and broadly U-shaped. The fixation of the specimen does not permit examination of the inner anatomy of the stomach. Judging from the outer view (Figure 1G), the stomach has a small caecum and seemingly a single duct of the digestive gland, situated near the esophagus opening. Typhlosoles of even size can be seen through the stomach wall. The gland of Leiblein is large, greenish-gray in fixed specimen, tubular, coiled anteriorly and simple posteriorly. In the posterior part, the transverse folds are seen through the gland wall. The gland opens into the esophagus through a duct without defined constriction (Figure 1H).

The salivary glands are paired, approximately equal-sized, rather large and loose, situated on both sides of rhynchodaeum, partially covering it dorsally and laterally. When the organs of the haemocoel are extended, the glands lie at both sides of the valve of Leiblein. Immediately after leaving the glands, the salivary ducts enter the walls of the esophagus in front of the valve of Leiblein. There is a single, long, tubular accessory salivary gland, partially embedded in the right primary salivary gland. Gland histology is typical for neogastropods, consisting of a thick outer epithelial layer and thin inner ones, delimited with a layer of circular muscle fibers.

The highly concentrated circumesophageal nerve ring is situated in the position typical for Muricoidea, just posterior to the valve of Leiblein.

Male reproductive system: The sectioned specimen was a mature male. The penis is long, occupying nearly the whole length of mantle cavity, narrow, with a deeply concave anterior surface and small conical papillae (Figure 1I). It is possible that the concavity is an artifact due to fixation. The seminal duct is open while running on the floor of mantle cavity toward the penis base, and deeply embedded and nearly closed in the penis body. A very narrow slit follows along the inner side of the penis and connects the duct with the exterior.

Ceratoxancus elongatus

The dissected specimen (New Caledonia, MUSORSTOM 4, sta. CP199) has a shell length of 23.7 mm, last teleoconch whorl length 15.4 mm, aperture length 8.2 mm, siphonal canal length 2.5 mm, shell diameter 8.8 mm. The operculum is vestigial (checked in two specimens) (Figure 4C), oval, and about 1 mm in length (i.e., less than 12% of aperture length). The foot is attached on nearly the whole surface of the operculum. The mantle edge is slightly scalloped but lacks a pronounced lobe corresponding to the labral spine.

The odontophore with radula lies completely outside the retracted proboscis. The radula (Figure 3C, D) is about 2.3 mm long (9.7% of shell length and 28% of aperture length) and about 130 μm broad (0.54% of shell height and 1.58% of aperture length), consisting of about 145 transverse rows. The rachidian basal parts have a shallowly arched anterior edge and a semi-rounded posterior edge, which is overlapped by the following tooth (Figure 3D), each bearing three nearly equal-sized short, blunt cusps, emanating from close to the anterior edge of the basal part. Lateral teeth are unicuspid, relatively much smaller than in *C. teramachii* and with a shorter base. The length of the lateral tooth base is 0.38× the width of the rachidian.

The gland of Leiblein is a little smaller than in *C. teramachii*.

The dissected specimen was a mature male. The long penis lacks a defined papilla.

Ceratoxancus ***melichrous*** sp. nov.

The dissected specimen (Norfolk Ridge, BATHUS 3, sta. DW 776) has a shell length of 18.6 mm, last teleoconch whorl length 12.4 mm, aperture length 6.5 mm, shell diameter 6.8 mm.

External anatomy: The upper body was torn off during extraction from the shell. The remaining part is pale yellowish and consists of two whorls (Figure 4A, B), the mantle spanning one whorl, the nephridium 0.3 whorl. The operculum is rather large, thin, transparent and yellow, elongate leaf-shaped and slightly recurved, occupying 0.5× aperture length. The columellar muscle is attached in the upper third of the operculum. The siphon is short, simple, and pale greyish. The columellar muscle is very thick with two deep grooves corresponding to the columellar teeth. The mantle edge is even, without lobe. The mantle is thin, and the ctenidium and osphradium are clearly visible through it. The head is broad with short stout tentacles and large eyes.

The salivary glands are completely fused, situated on the left side of the proboscis sac, and totally envelop the valve of Leiblein. The salivary ducts are paired. The mid-esophagus is at least twice as short as in *C. teramachii*. The gland of Leiblein has less pronounced tubular form than in *C. teramachii* and is not coiled in the anterior part. The accessory salivary gland was not found in the specimen dissected, although it may have been present and embedded in the primary salivary gland. The odontophore is contained within the retracted proboscis, but the radula sac is slightly protruding beyond its rear end.

The radula (Figure 2E, F) is about 2.4 mm in length (12.9% of shell length and 36.9% of aperture length) and

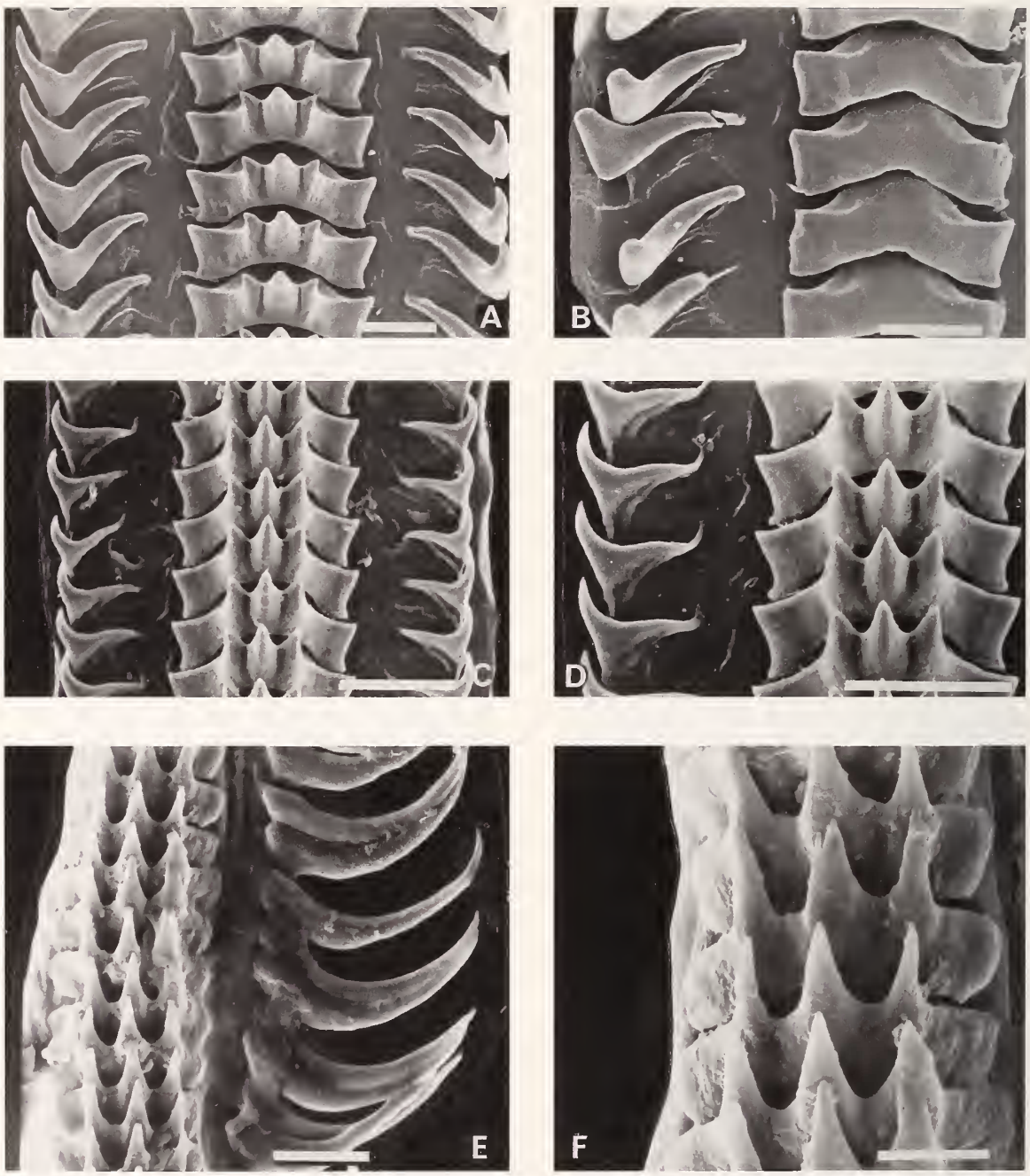


Figure 3

Radulae of *Ceratoxancus* spp. *Ceratoxancus* ***basileus*** Kantor & Bouchet, sp. nov. (A–B) (BIOCAL sta. DW33): A, dorsal view of the radular ribbon; B, enlarged posteriormost part of the ribbon, showing the worn rachidian and lateral teeth. *Ceratoxancus elongatus* (C–D) (MUSORSTOM 4, sta. CP199): C, dorsal view of the radular ribbon; D, enlarged rachidian and lateral teeth. *Ceratoxancus* ***niveus*** Kantor & Bouchet, sp. nov. (E, F) (BIOCAL, sta. DW 51): E, dorsal view of the half of radular ribbon; F, enlarged rachidian teeth. Scale bars 50 μm (A, B, C, D); 20 μm (E); 10 μm (F).

about 186 μm broad (1.0% of shell height and 2.86% of aperture length), consisting of about 130 transverse rows, and is relatively wider than in the other species. The rachidians (Figure 2F) have a shallowly arched anterior edge of the basal part, three sharp, rather long cusps, emanating from the posterior edge, the central cusp the longest. Lateral teeth are unicuspid, long, with a short base. Length of the lateral tooth base is 0.47 × the width of the rachidian.

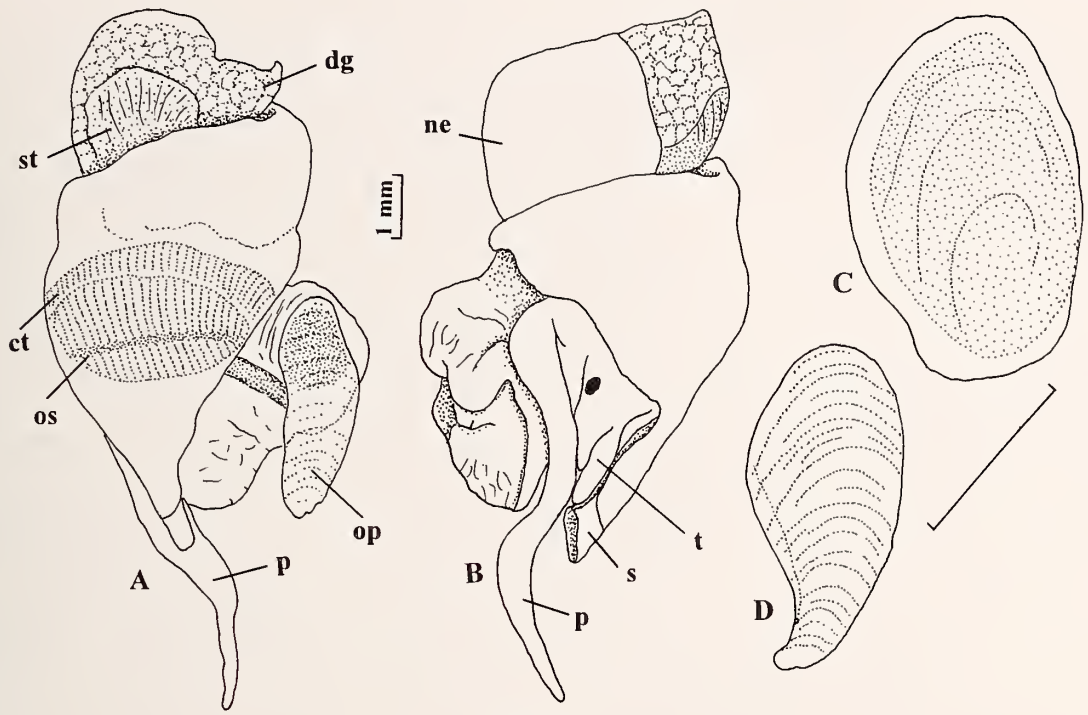


Figure 4

A–B, *Ceratoxancus* ***melichrous*** Kantor & Bouchet, sp. nov. (BATHUS 3, sta. DW 776, shell height 18.6 mm): body, removed from the shell; C, operculum of *C. elongatus* (MUSORSTOM 4, sta. CP199, shell length of 23.7 mm); D, operculum of *C.* ***niveus*** Kantor & Bouchet, sp. nov. (BIOCAL, sta. DW 51, shell height 9.35 mm). Scale bars 0.5 mm (C), 1 mm (D).

Male reproductive system: The penis is long, protruding anteriorly in the studied specimen, rather narrow, tapering anteriorly, and without a pronounced papilla.

Ceratoxancus ***niveus*** sp. nov.

The specimen with dried body (Norfolk Ridge, BIOCAL, sta. DW 51) has a shell length of 9.35 mm, last teleoconch whorl length 6.2 mm, aperture length 3.9 mm, shell diameter 3.5 mm. The body was softened in potassium bicarbonate and extracted from the shell.

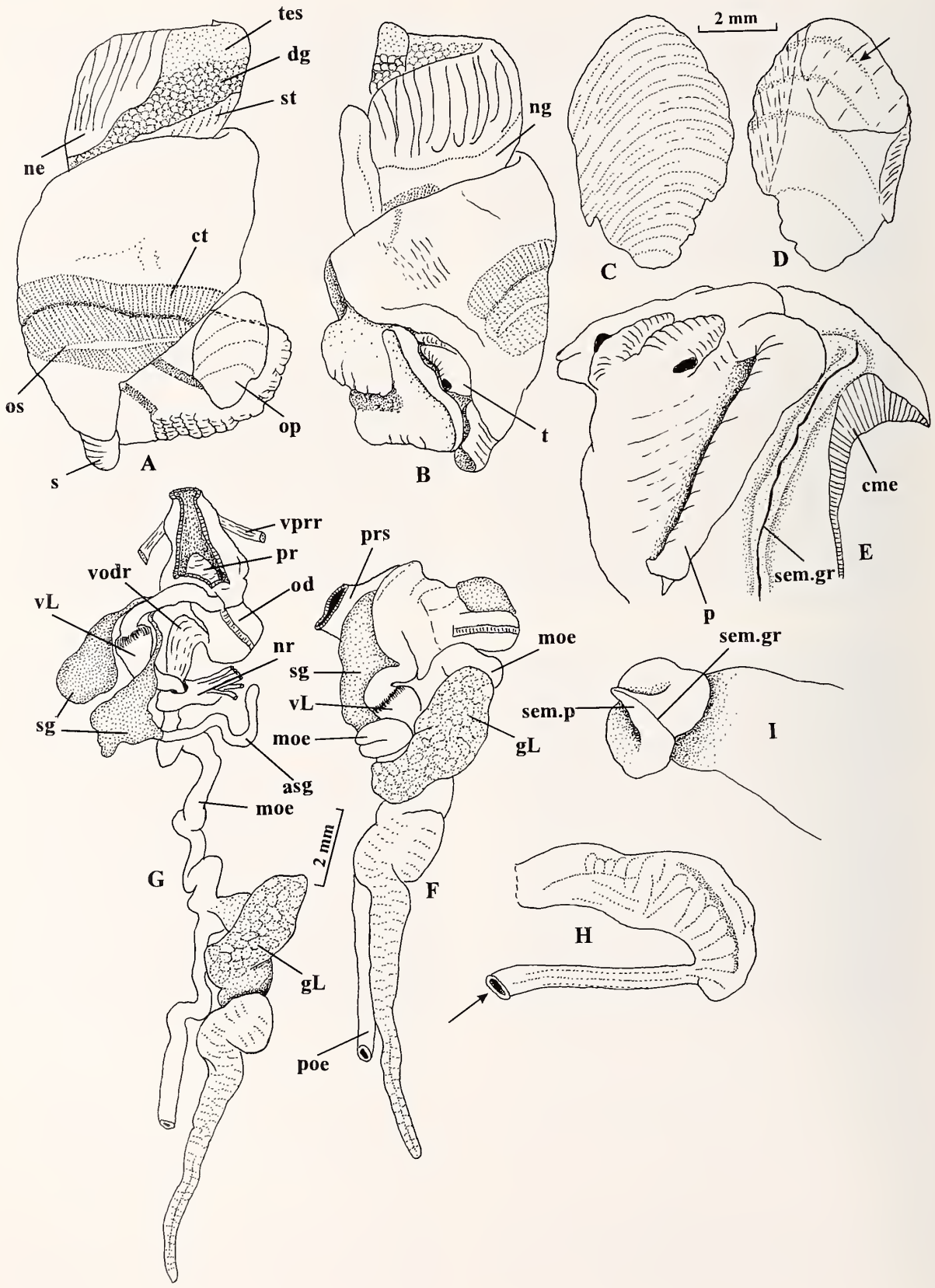
The operculum is medium-sized, leaf-shaped, with the nucleus turned to the left (Figure 4D), and occupies 0.45× the aperture length. The large eyes are situated at the base of long and narrow cephalic tentacles. The specimen is an adult male, the penis is long and flattened, apparently with an open seminal groove, and lacking a pronounced seminal papilla. The proboscis (protruding through the mouth opening) is medium-long, thick at the tip, narrowing toward the mouth opening. The odontophore with radula is situated at the proboscis tip.

The radula (Figure 3E, F) is narrow, width about 69 μm (0.73% of shell height and 1.76% of aperture length). The rachidian (Figure 3F) basal part has a nearly straight anterior edge and three equal, widely spaced, sharp, and rather long cusps, emanating from the posterior edge. The lateral teeth are unicuspid and long, with a very short base, length of the base 0.27× the width of the rachidian.

Ceratoxancus ***basileus*** sp. nov.

The dissected specimen (New Caledonia, BIOCAL, sta. DW33) is 48.1 mm high, diameter 17.5 mm, last whorl height 31.5 mm, aperture height 16.8 mm.

External anatomy (Figure 5A, B): The upper body whorls were torn off during extraction from the shell. The remaining part is pale yellowish and consists of 2.25 whorls, the mantle spanning 1.2 whorls, the nephridium 0.4 whorl. The operculum is medium-sized, occupying 0.37× aperture length (lower part of the operculum with nucleus damaged), oval, thin, semi-transparent, and yellow-brown (Figure 5C, D). The columellar muscle is attached to the upper third of the operculum. The foot is rather long (L/W ≈ 2.3). The siphon is rather short and simple. The columellar muscle is thick with two deep grooves, corresponding to columellar plaits. The mantle has a thickened edge, but is thin posteriorly, and the mantle organs are clearly visible through it. Due to the high retraction of the animal inside the shell, the mantle partially covers the head. The head is narrow with short stout tentacles and large eyes. The border between the mantle cavity and the nephridium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is represented by a deep cleft. The nephridium consists of 13 vertical lamellae, which are visible through its wall.

Mantle: The ctenidium is very long and occupies 0.9× mantle length, narrow (L/W ≈ 9.5), with high hanging leaflets. The osphradium is large, 0.5× as long and 2× as wide as the ctenidium, asymmetrical, with the right side 1.5× broader than the left. The hypobranchial gland is covered with a thick mucus layer and is transversely pleated. The anal gland is absent.

Digestive system: The organs of the body haemocoel are compact (Figure 5F). The proboscis in the contracted state is extremely short (less than 1 mm), smooth, and occupies only about ¼ of the rhynchodeal cavity. The rhynchodaeum (= proboscis sheath) is thick-walled and lined with tall epithelium.

The paired, rather thin muscles, functioning as ventral proboscis retractors, are attached latero-ventrally to the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel. This probably indicates that all the rhynchodaeum takes part in the proboscis evertion, and in the completely everted position of the proboscis, these retractors are attached to the inner wall of proboscis.

The buccal mass is very large and muscular, situated beyond the base of the retracted proboscis. The radular diverticulum opens into the buccal cavity at the proboscis base in its contracted state. The odontophoral subradular cartilages are paired, not fused anteriorly, but connected with transverse muscle. They are 1.5× shorter than the radular sac. The large ventral odontophoral retractor passes through the nerve ring, follows the bottom of the cephalic haemocoel, and joins the columellar muscle.

The radula (Figure 3A, B) is about 5.5 mm in length (11% of shell length and 33% of aperture length) and about 430 μm broad (0.89% of shell height and 2.55% of aperture length), and consists of about 140 transverse rows. The rachidian teeth have a shallowly arched anterior edge on the basal part, and a semi-rounded posterior edge, slightly overlapped by the following tooth (this is more clearly seen on the most distal part of the radula where the cusps are worn off, Figure 3B), with a short, blunt, and thick median cusp and two much thinner lateral cusps emanating close to the anterior edge of the basal part. Lateral teeth are unicuspid, with a long narrow base, length of tooth base 0.65× the width of the rachidian base.

After leaving the proboscis, the esophagus soon opens into the valve of Leiblein (Figure 5G). Between the valve and the opening of the gland of Leiblein, the esophagus is significantly widened and glandular. This part, representing the mid-esophagus, is very long and convoluted. When the organs of the haemocoel are stretched by dissection, the glands lie on both sides of the valve of Leiblein, which is well defined, much broader than the esophagus, and pyriform, with a conical ciliary valve. The non-glandular posterior esophagus is rather thin, runs along the left side of the gland of Leiblein, and opens into the stomach.

The thin-walled, broadly U-shaped stomach is rather large by comparison to the anterior foregut. The fixation of the specimen does not permit an examination of its inner anatomy. Judging from the external view (Figure 5H), the stomach has a very small caecum and a single duct of the digestive gland, situated near the esophageal opening. The gland of Leiblein is large, pale greenish anteriorly, thin-walled, tubular, coiled anteriorly and simple posteriorly; it opens into the esophagus through a duct without distinct constriction. Acini are clearly seen through the gland.

The salivary glands are paired, approximately equal-sized, medium-sized, surrounding the rhynchodaeum and the buccal mass. When the organs of the haemocoel are extended, the glands lie on both sides of the valve of Leiblein. They narrow toward the short ducts, which enter the walls of the esophagus in front of the valve of Leiblein. There is a single long, tubular accessory salivary gland, partially embedded in the right primary salivary gland.

The highly concentrated circumesophageal nerve ring is situated in the position typical for Muricoidea, just posterior to the valve of Leiblein.

Male reproductive system: The penis is moderately short, occupying less than half the length of the mantle cavity, narrow, and very flattened, with a flattened anterior surface and distinct conical papilla. The seminal duct opens while running on the floor of the mantle cavity toward the penis base (Figure 5E), and is deeply embedded in the penis body. A very narrow slit follows for a short distance along the inner side of the penis and probably connects the duct with the exterior. For most of the penis length, the duct seems to be closed and becomes open again at the base of the papilla (Figure 5I).

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Figure 5

Ceratoxancus ***basileus*** Kantor & Bouchet, sp. nov. (BIOCAL, sta. DW33, shell height 48.1 mm). A, B, body, removed from the shell; C, D, operculum (C, from outer side, D, from inner side, an arrow indicates the place of attachment of the columellar muscle); E, anterior part of the body, mantle removed to show the penis; F, organs of the body haemocoel in natural position; G, organs of the body haemocoel, expanded. Proboscis sac opened to show the proboscis; H, outer view of the stomach, same scale as F, G; I, tip of the penis.

SYSTEMATICS

Genus *Ceratoxancus* Kuroda, 1952

Type species: (by monotypy) *Ceratoxancus teramachii* Kuroda, 1952.

Ceratoxancus teramachii Kuroda, 1952

(Figures 1, 2A–D, 6A–J, 8C, D)

Ceratoxancus teramachii Kuroda, 1952:70–71 (30–31), figs. 1–4.

Ceratoxancus teramachii: Sakurai, 1958: figs. 3, 4; Cernohorsky, 1973:131, fig. 16; Cernohorsky, 1977:28, fig. 2; Higo & Goto, 1993:274.

NOT *Ceratoxancus teramachii:* Shikama & Horikoshi, 1963: 95, pl. 76, fig. 4; Habe, 1964:104, pl. 33, fig. 21.

Type material: Holotype in Toba Aquarium (not seen); 1 paratype AMNH 169039.

Type locality: Off Kii Peninsula, Japan.

Material examined: JAPAN. Off Tosa, 365 m, 1 lv, paratype (AMNH 169039). Off Tosa, 275 m, 1 lv (AMNH 169026).

CORAL SEA. MUSORSTOM 5: R/V *Coriolis.* CHESTERFIELD PLATEAU. Sta. DW337, 19°54′S, 158°38′E, 412–430 m, 1 lv adult (dissected). Sta. DW338, 19°52′S, 158°40′E, 540–580 m, 1 lv subadult (sectioned). Sta. DC378, 19°54′S, 158°38′E, 355 m, 1 lv. Sta. DC379, 19°53′S, 158°40′E, 370–400 m, 1 lv. Sta. CP389, 20°45′S, 160°54′E, 500 m, 1 lv subadult. ARGO BANK. Sta. DW300, 22°48′S, 159°24′E, 450 m, 1 lv subadult. Sta. DW306, 22°08′S, 159°21′E, 375–415 m, 1 dd.

NEW CALEDONIA. BIOCAL: R/V *Jean-Charcot,* sta. DW66, 24°55′S, 168°22′E, 505–515 m, 1 dd. BIOGEOCAL: R/V *Coriolis,* sta. DW253, 21°32′S, 166°29′E, 310–315 m, 1 dd. SMIB 3: R/V *Vauban,* sta. DW1, 24°56′S, 168°22′E, 520 m, 1 lv, 4 dd. Sta. DW2, 24°53′S, 168°22′E, 530–537 m, 1 dd. Sta. DW5, 24°55′S, 168°22′E, 502–512 m, 1 lv, 1 dd. Sta. DW6, 24°56′S, 168°21′E, 505 m, 1 lv. Sta. DW7, 24°55′S, 168°21′E, 505 m, 1 dd. BERYX 11: R/V *Alis,* sta. DW10, 24°53′S, 168°21′E, 565–600 m, 1 dd. Sta. DW40, 23°41′S, 168°01′E, 240–300 m, 1 dd. SMIB 8: R/V *Alis,* sta. DW146–147, 24°55′S, 168°22′E, 508–532 m, 1 lv, 2 dd. Sta. DW149, 24°55′S, 168°22′E, 508–510 m, 2 dd. Sta. DW150, 24°54′S, 168°22′E, 519–530 m, 1 lv, 1 dd. Sta. DW152, 24°54′S, 168°22′E, 514–530 m, 1 lv, 2 dd. Sta. DW169, 23°37′S, 167°42′E, 447–450 m, 1 lv. BATHUS 3: R/V *Alis,* sta. DW817, 23°42′S, 168°16′E, 405–410 m, 1 dd. BATHUS 4: R/V *Alis,* sta. DW918, 18°49′S, 163°16′E, 613–647 m, 1 dd.

LOYALTY RIDGE. MUSORSTOM 6: R/V *Alis,* sta. DW471, 21°08′S, 167°54′E, 460 m, 1 dd. Sta. DW478, 21°09′S, 167°54′E, 400 m, 1 dd.

VANUATU. MUSORSTOM 8: R/V *Alis,* sta. DW977, 19°25′S, 169°29′E, 410–505 m, 1 dd.

Distribution: Off Kii and Tosa, Japan, in ca. 275–365 m, Hawaii, in 340–375 m; new records from the Coral Sea, New Caledonia, Loyalty Islands, and Vanuatu, alive in 355–540 m.

Description: (based on material from New Caledonia and the Chesterfield Plateau) Shell ovoid, fusiform, solid, consisting of 2.5 protoconch and up to 7.5 moderately convex teleoconch whorls. Protoconch I smooth, with large nucleus, diameter 375 μm; protoconch II consisting of two whorls, first whorl smooth, second whorl with an adapical row of granules, a basal keel that is just covered by the successive whorl, and six strong opisthocyrt axial ribs before the protoconch/teleoconch boundary. Early teleoconch whorls flat-sided, later whorls moderately convex, with moderately to deeply channeled suture. Sculpture consisting of strong orthocline ribs crossed by weaker spiral grooves, and much finer incremental lines, 11–14 very distinct and strong ribs per whorl on first three whorls, more numerous but gradually fading on subsequent whorls. Last adult whorl with low, broad, and indistinct axial varices. Spiral sculpture not sharply defined, apart from one or two stronger grooves at shoulder, and ca. 12 well-defined cords on base of last adult whorl. Incremental scars of labral spine forming deep sulcus with raised edges on base of last whorl. Aperture ovoid, elongate, comprising ca. 46–51% of total shell height. Outer lip thin, straight, with strongly projecting labral spine. Siphonal canal broad, very short. Inner lip with very thin, glossy callus. Columella with three plaits, adapical one strongest.

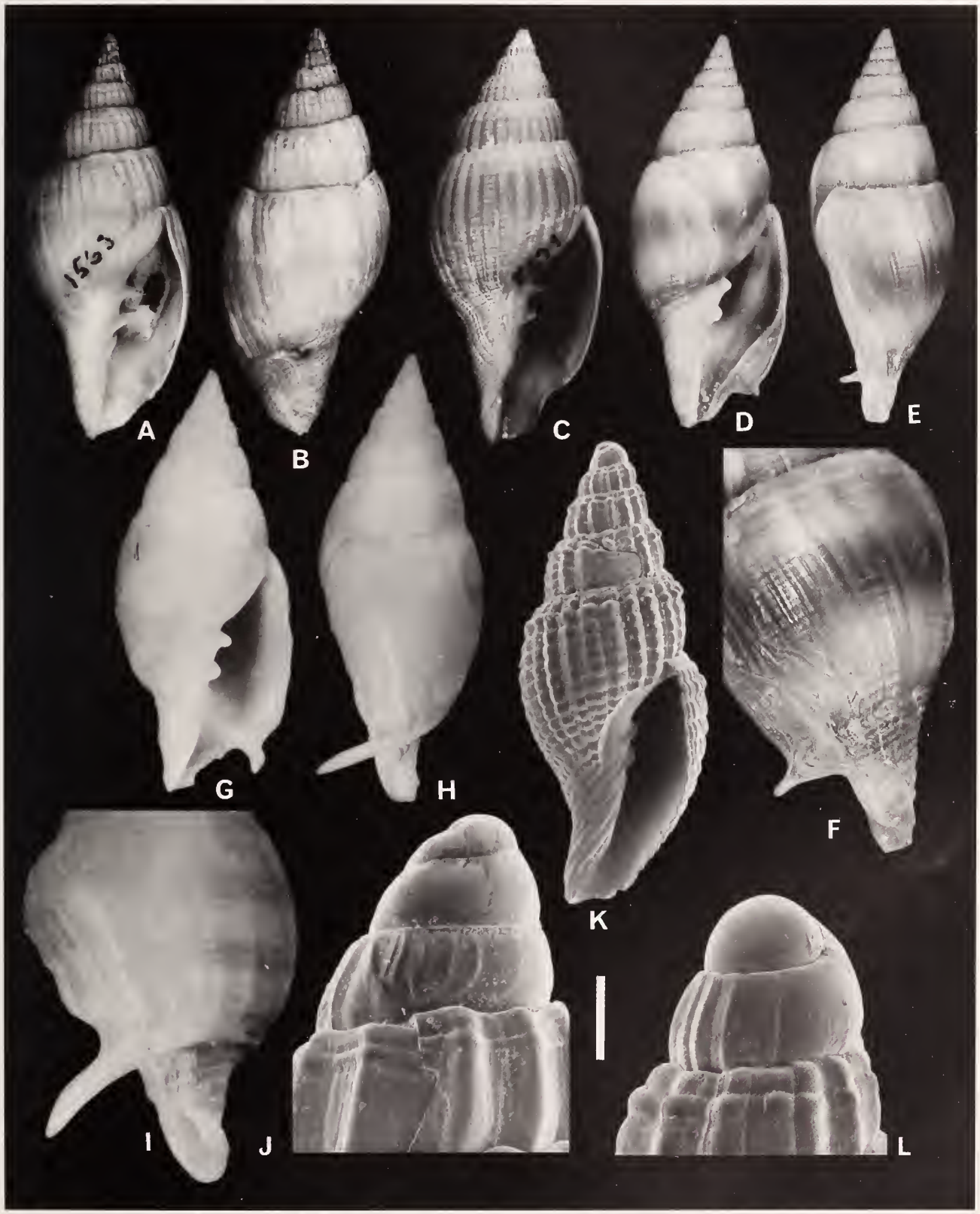
Specimens from New Caledonia have a yellowish-tan background color and three brown spiral bands with indistinct margins: a narrow adapical one, a broader one at periphery, and one encircling the labral sulcus. Specimens from the Coral Sea are uniformly grayish beige without spiral bands. Protoconch pale yellowish. Periostracum thin, light yellowish gray.

Dimensions of largest adult: shell length 31.5 mm, last teleoconch whorl length 21.5 mm, aperture length 14.0

→

Figure 6

Ceratoxancus teramachii (A–J). A, B, paratype, 30 mm (AMNH 169039); C, Japan, off Tosa, 275 m (AMNH 169026), 30 mm; D–F, New Caledonia (SMIB3, sta. DW5), 30.0 mm, F, labral spine; G–I, Coral Sea (MUSORSTOM5, sta. 379), 28.7 mm, I, labral spine; J, protoconch (MUSORSTOM5 sta. 306). *Ceratoxancus niveus* (K, L), K, holotype, 8.8 mm; L, protoconch of paratype (BIOCAL, sta. DW51). Scale bar (protoconchs) 500 μm.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mm, siphonal canal length 3.6 mm, shell diameter 12.6 mm.

Remarks: Our specimens from the southwest Pacific match the original description and material from Japan (illustrated by Sakurai, 1958: figs. 3, 4, and material in AMNH). In Japan, however, the axial sculpture may persist onto the last adult whorl; such sculptured specimens superficially resemble *C. elongatus* and have been confused with it (see below under that species).

In the majority of specimens, the outer lip is broken and thus the labral spine is absent. Nevertheless, in four specimens with intact outer lip, the degree of prominence of the labral spine varies greatly (Figure 6) from a discrete rounded or triangular projection to a very long, sharp spine with a length reaching 30% of aperture length.

Ceratoxancus elongatus Sakurai, 1958

(Figures 3C, D, 4C, 7A–D, 8A, B)

Ceratoxancus elongatus Sakurai, 1958: 161, figs. 1, 2.
Ceratoxancus elongatus: Habe, 1961:68, pl. 33, fig. 21; Cernohorsky, 1973:130; Hasegawa & Saito, 1995:29, pl. 5, fig. 4.
Ceratoxancus teramachii: Shikama & Horikoshi, 1963:95, pl. 76, fig. 4; Habe, 1964:104, pl. 33, fig. 21.

Type material: Holotype in National Science Museum, Tokyo, NSMT-Mo 70251 (illustrated by Hasegawa & Saito, 1995).

Type locality: Off Tosa, Japan, "from a somewhat deep bottom but the exact depth is not known."

Material examined: NEW CALEDONIA. BIOCAL: R/V *Jean-Charcot,* sta. DW51, 23°05′S, 167°45′E, 680–700 m, 2 lv, 1 dd. Sta. DW66, 24°55′S, 168°22′E, 505–515 m, 2 lv, 3 dd. MUSORSTOM 4: R/V *Vauban,* sta. DW159, 18°46′S, 163°16′E, 585 m, 2 dd. Sta. DW196, 18°55′S, 163°24′E, 460 m, 1 dd. Sta. CP199, 18°50′S, 163°14′E, 595 m, 1 lv (dissected). CHALCAL 2: R/V *Coriolis,* sta. DW72, 24°55′S, 168°22′E, 527 m, 3 lv, 3 dd. Sta. DW74, 24°40′S, 168°38′E, 650 m, 3 dd. SMIB 3: R/V *Vauban,* sta. DW1, 24°56′S, 168°22′E, 520 m, 1 dd. Sta. DW2, 24°53′S, 168°22′E, 530–537 m, 1 dd. Sta. DW3, 24°55′S, 168°22′E, 513 m, 1 lv. Sta. DW5, 24°55′S, 168°22′E, 502–512 m, 1 dd. Sta. DW7, 24°55′S, 168°21′E, 505 m, 1 dd. BERYX 11: R/V *Alis,* sta. DW39, 23°37′S, 167°40′E, 490–500 m, 1 dd. SMIB 8: R/V *Alis,* sta. DW146–147, 24°55′S, 168°22′E, 508–532 m, 1 lv, 1 dd. Sta. DW148, 24°56′S, 168°21′E, 510 m, 1 dd. Sta. DW149, 24°55′S, 168°22′E, 508–510 m, 4 dd. Sta. DW152, 24°54′S, 168°22′E, 514–530 m, 1 lv, 2 dd. BATHUS 2: R/V *Alis,* sta. DW721, 22°54′S, 167°17′E, 525–547 m, 1 lv. BATHUS 3: R/V *Alis,* sta. DW809, 23°39′S, 167°59′E, 650–730 m, 5 dd. Sta. DW825, 23°22′S, 168°00′E, 597–605 m, 1 dd. BATHUS 4: R/V *Alis,* sta. DW918, 18°49,02′S, 163°15,80′E, 613–647 m, 1 dd. R/V *Alis,* sta. CP922, 18°48′S, 163°19′E, 600 m, 1 dd.

LOYALTY RIDGE. MUSORSTOM 6: R/V *Alis,* sta. DW468, 21°06′S, 167°33′E, 600 m, 1 dd. Sta. DW483, 21°20′S, 167°48′E, 600 m, 1 lv. BATHUS 3: R/V *Alis,* sta. DW776, 24°44′S, 170°08′E, 770–830 m, 2 dd. Sta. DW778, 24°43′S, 170°07′E, 750–760 m, 1 lv. Sta. DW781, 23°54′S, 169°46′E, 625–640 m, 2 dd. Sta. DW786, 23°54′S, 169°49′E, 699–715 m, 1 dd. Sta. DW787, 23°54′S, 169°48′E, 695–702 m, 1 dd. Sta. DW790, 23°49′S, 169°48′E, 685–715 m, 1 dd. Sta. DW794, 23°48′S, 169°49′E, 751–755 m, 1 dd.

VANUATU. MUSORSTOM 8: R/V *Alis,* sta. DW1128, 16°02′S, 166°38′E, 778–811 m, 1 dd.

KERMADEC ISLANDS. R/V *Akademik Nesmeyanov,* 30°28.0′S, 178°37.2′W, 1000 m, 1 dd (NMNZ M249892).

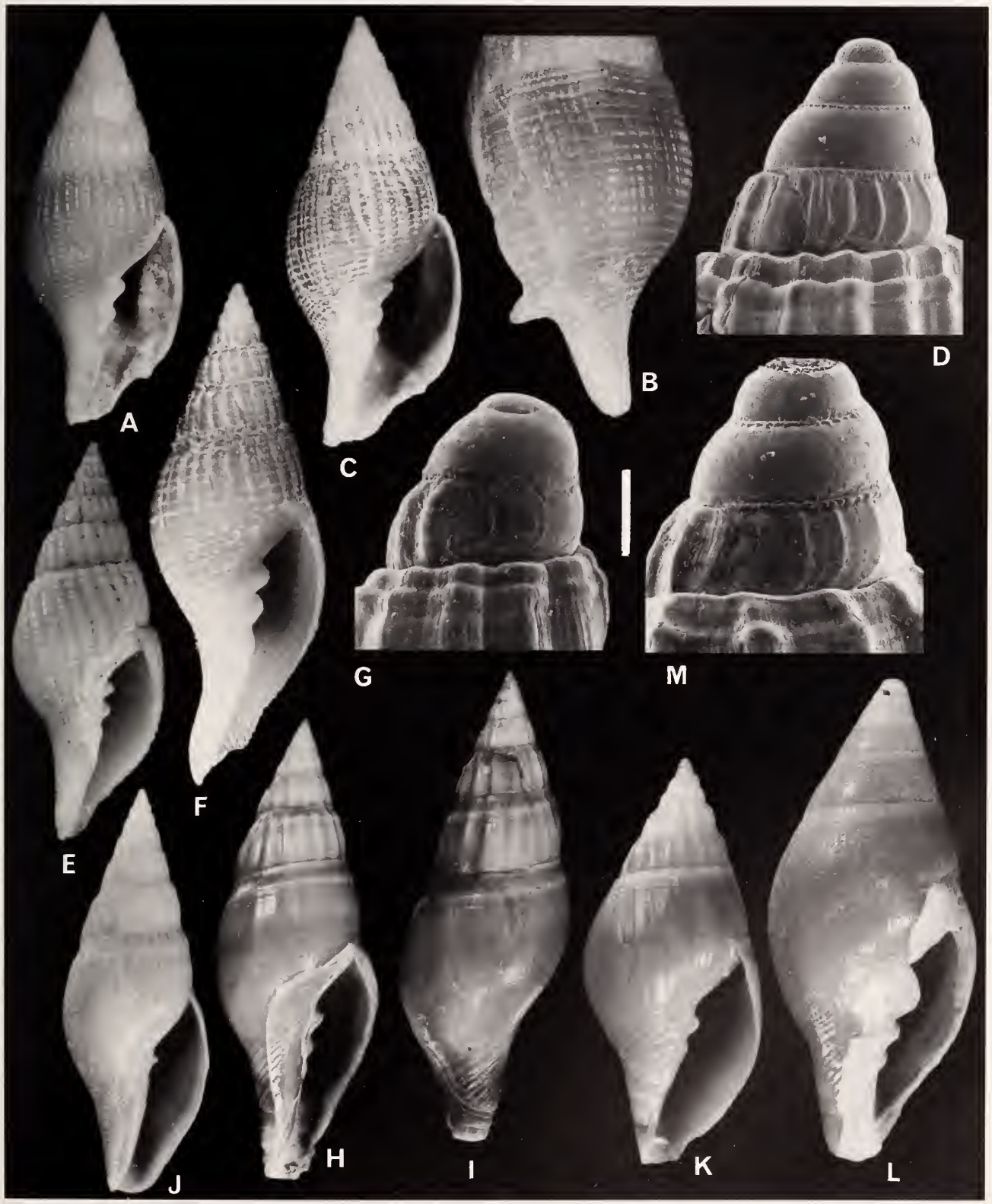
Distribution: Off Tosa, Japan; new records from New Caledonia, Loyalty Ridge, Vanuatu, and Kermadec Islands, alive in 515–750 m, shells in 460–1000 m.

Description: (based on material from New Caledonia). Shell slender, fusiform, solid, consisting of 2.5 protoconch and up to 7+ moderately convex teleoconch whorls. Protoconch I smooth, with large nucleus, diameter 325 μm; protoconch II consisting of two whorls, smooth with a narrow adapical band of irregular tubercules, a basal keel that is just covered by successive whorls, and six to nine strong opisthocyrt axial ribs before the protoconch/teleoconch boundary. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong orthocline ribs crossed by distinct spiral grooves, producing a muricated appearance. Number of axial ribs increasing from ca. 15 on the first teleoconch whorl to 32–40 on adult whorls, where they are broader and less sharply defined.

→

Figure 7

Ceratoxancus elongatus (A–D). A, New Caledonia (MUSORSTOM 4, sta. DW159), 20.4 mm; B, labral spine of the same specimen; C, New Caledonia (BIOCAL, sta. DW66), 18.5 mm; D, protoconch (BIOCAL, sta. DW51). *Ceratoxancus* ***melichrous*** Kantor & Bouchet, sp. nov. (E–G), E, holotype, 20.4 mm; F, New Caledonia (BATHUS 3, sta. DW776), 21.8 mm; G, protoconch of paratype (BATHUS 3, sta. DW 776). *Ceratoxancus* ***basileus*** Kantor & Bouchet, sp. nov. (H–J), H, I, holotype (dead collected shell without periostracum), 56.1 mm; J, New Caledonia (BIOCAL, sta. DW33, live collected shell with periostracum), 48.1 mm. *Ceratoxancus* ***leios*** Kantor & Bouchet, sp. nov. (K–M), K, holotype, 21.0 mm; L, New Caledonia (SMIB 8, sta. DW193–196), 38.0 mm; M, protoconch of holotype. Scale bar (protoconchs) 500 μm.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Exposed part of early spire whorls with four or five incised grooves, of which one or two at shoulder are stronger. About 25 grooves on last adult whorl, plus 15, more closely set, on base and canal. Incremental scar of the labral spine similar to other grooves beside it. Aperture ovoid, elongate, comprising ca. 42–46% of total shell height. Outer lip thin, straight, with small projecting labral spine. Siphonal canal broad, short. Inner lip with thin, glossy callus. Columella with three plaits, the adapical one stronger.

Color uniform brown, periostracum very thin, transparent.

Dimensions of largest adult (protoconch, and part of first teleoconch whorl, missing): height 32.2 mm, last whorl height 22.5 mm, aperture height 12.0 mm, siphonal canal length 6.5 mm, diameter 12.6 mm.

Remarks: The New Caledonia specimens match the original description of *Ceratoxancus elongatus*. They differ from *C. teramachii* by the more narrow proportions, more convex outer lip, impressed suture, reticulated sculpture extending to the last adult whorl, and shorter labral spine. There is no doubt that two species are involved, and *Ceratoxancus elongatus* must be removed from the synonymy of *C. teramachii*. The two species co-occur in the same area of the Norfolk Ridge (ca. 24°55′–25°00′S, 168°20′E) and have even been taken together in the same haul (BIOCAL sta. DW66). Moreover, both species differ greatly in the operculum morphology. While in *C. teramachii* the operculum is medium-sized with terminal nucleus occupying at least 0.4× aperture length, in *C. elongatus* it is vestigial with subcentral nucleus, and occupies less that 0.13× aperture length.

Japanese authors have persistently confused the two species of *Ceratoxancus*. Habe (1961: pl. 33, fig. 21) illustrated a specimen (the holotype according to Hasegawa & Saito, 1995: 29) of *C. elongatus* under that name, but the same shell was subsequently identified as *C. teramachii*, with the comment that *C. elongatus* is "an elongate form" of it (Habe, 1964: 104). Shikama & Horikoshi's (1963: pl. 76, fig. 4) illustrated specimen of *C. teramachii* also belongs to *C. elongatus*. Habe's synonymization appears to have been followed to this day in the Japanese literature (Higo & Goto, 1993).

Ceratoxancus ***melichrous*** Kantor & Bouchet, sp. nov.

(Figures 2E, F, 4A, B, 7E–G)

Type material: Holotype and 1 paratype in MNHN.

Type locality: New Caledonia, Norfolk Ridge, SMIB 4: R/V *Alis*, sta. DW39, 24°56′S, 168°22′E, 525–560 m.

Material examined: CHALCAL 2: R/V *Coriolis*, sta. DW72, 24°54′S, 168°22′E, 527 m, 1 dd. SMIB 4: R/V *Alis*, sta. DW39, 24°56′S, 168°22′E, 525–560 m, 1 dd (holotype). SMIB 8: R/V *Alis*, sta. DW150, 24°54′S, 168°22′E, 519–530 m, 1 dd. Sta. DW152, 24°54′S, 168°22′E, 514–530 m, 2 dd. BATHUS 3: R/V *Alis*, sta. DW776, 24°44′S, 170°08′E, 770–830 m, 3 lv (1 paratype, 1 dissected).

Distribution: New Caledonia: Norfolk Ridge, alive in 770–830 m, shells from 530 m.

Description: (holotype; description of protoconch based on paratype) Shell slender, fusiform, solid, consisting of 1.5 protoconch and seven moderately convex teleoconch whorls. Protoconch (present but corroded in holotype) paucispiral, diameter 650 μm, with small initial nucleus; smooth with a basal keel that is just covered by successive whorl, and one strong opisthocyrt varix marking the protoconch/teleoconch boundary. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong prosocline ribs crossed by distinct spiral grooves, producing a coarsely muricated appearance. Number of axial ribs increasing from 14 on the first teleoconch whorl to 25 on last adult whorl, where they are broader and less sharply defined in the last half-whorl before peristome. Exposed part of spire whorls with five incised grooves, which delimit a stronger spiral cord at shoulder. About 15 grooves on last adult whorl, plus 22, more closely set, on base and canal. No labral spine fasciole. Aperture ovoid, elongate, comprising ca. 34% of total shell height. Outer lip (damaged in holotype) thin, simple. Siphonal canal narrow, short, but distinctly set off. Inner lip with rather thick callus. Columella with three plaits, adapical one stronger.

Color uniform light yellowish brown, periostracum very thin, transparent.

Dimensions: height 20.4 mm, last whorl height 14.1 mm, aperture height 7.0 mm, siphonal canal length 4.4 mm, diameter 7.8 mm.

Remarks: *Ceratoxancus* ***melichrous*** is superficially very similar to *C. elongatus* but differs by: (a) its paucispiral protoconch, indicating non-planktotrophic development (vs. multispiral, indicating planktotrophic development in *C. elongatus*); (b) its coarser sculpture; (c) the lack of labral spine and/or labral spine fasciole; (d) its lighter color and smaller adult size. Even in the absence of a protoconch, the combination of coarse sculpture and light yellowish color permits identification of *C.* ***melichrous***. Anatomically, *C.* ***melichrous*** differs from *C. elongatus* in having a shorter mid-esophagus and a gland of Leiblein that is not coiled in the anterior part.

C. ***niveus***, which also has a paucispiral protoconch, differs by its finer sculpture, smaller adult size, and off-white color.

Etymology: *melichrous*, a Greek word meaning colored like honey.

Ceratoxancus ***niveus*** Kantor & Bouchet, sp. nov.

(Figures 3E, F, 4D, 6K, L)

Type material: Holotype (lv) and 5 paratypes (2 lv, 3 dd) in MNHN.

Type locality: New Caledonia, Norfolk Ridge, BIOCAL: R/V *Jean-Charcot,* sta. DW51, 23°05'S, 167°45'E, 680–700 m.

Material examined: Known only from the type material.

Description: (holotype) Shell slender, fusiform, solid, consisting of ca. one protoconch and 4.3 moderately convex teleoconch whorls. Protoconch paucispiral, diameter ca. 750 μm, with large nucleus, smooth; protoconch/teleoconch transition indistinct, six or seven strong axial ribs may belong to protoconch or teleoconch. Teleoconch whorls convex, with impressed suture. Sculpture consisting of strong prosocline ribs crossed by distinct spiral grooves, producing a coarsely muricated appearance. Number of axial ribs increasing from 15 on first teleoconch whorl to 27 on last adult whorl, where they remain sharply defined until behind the outer lip. Exposed part of spire whorls with four incised grooves, which delimit a stronger spiral cord at shoulder. About 20 grooves on last adult whorl, rather evenly spaced on shoulder, periphery and base, a little more crowded on canal. No labral spine fasciole. Aperture ovoid, elongate, comprising ca. 40% of total shell height. Outer lip sharp, thin, simple. Siphonal canal broad, short, indistinctly set off. Inner lip with narrow callus. Columella with three plaits, the abapical one almost indistinct.

Color uniform off-white, periostracum very thin, transparent.

Dimensions: height 8.8 mm, diameter 3.7 mm, last teleoconch whorl height 5.9 mm, aperture height 3.6 mm.

Remarks: *Ceratoxancus* ***niveus*** is separated from all other species of *Ceratoxancus* by the combination of small adult size, paucispiral protoconch, muricated sculpture, and white color. It most closely resembles *C.* ***melichrous*** but is distinguished by its large protoconch nucleus, finer sculpture, and color.

Etymology: *niveus,* Latin, snow white, in reference to the color of the shell.

Ceratoxancus ***leios*** Kantor & Bouchet, sp. nov.

(Figure 7K–M)

Type material: Holotype and 1 paratype in MNHN.

Type locality: New Caledonia, Norfolk Ridge. BATHUS 3: R/V *Alis,* sta. DW809, 23°39'S, 167°59'E, 650–730 m.

Material examined: NEW CALEDONIA. CHALCAL 2: R/V *Coriolis,* sta. DW74, 24°40'S, 168°38'E, 650 m, 1 dd. SMIB 8: R/V *Alis,* sta. DW193–196, 22°52'–23°00'S, 168°20'–168°22'E, 491–558 m, 1 dd (paratype). BATHUS 3: R/V *Alis,* sta. DW809, 23°39'S, 167°59'E, 650–730 m, 1 dd (holotype).

KERMADEC ISLANDS. R/V *Akademik Nesmeyanov,* 30°28.0'S, 178°37.2'W, 1000 m, 1 dd (NMNZ M249898).

Distribution: Norfolk Ridge and Kermadec Islands, shells only in 558–1000 m.

Description: (subadult holotype) Shell ovoid, fusiform, solid, consisting of 3+ (nucleus of protoconch I missing) protoconch and 5.5 moderately convex teleoconch whorls. Remaining part of protoconch I smooth, diameter 375 μm; protoconch II consisting of 2.5 whorls, smooth, with an adapical row of granules, a basal keel that is covered by successive whorls, and six widely spaced, strong, opisthocyrt axial ribs before the protoconch/teleoconch boundary. Adapical teleoconch whorls weakly shouldered, later whorls more flat-sided, with shallowly impressed suture. Sculpture consisting of strong orthocline ribs crossed by weaker spiral cords/grooves, and much finer incremental lines. There are 11 very distinct and strong ribs per whorl on the first three adapical whorls, more numerous but gradually fading on subsequent whorls. Last adult whorl with low, broad, and indistinct axial varices. Spiral sculpture well defined on first 3.5 whorls, consisting of one strong cord at shoulder, forming a nodulous intersection with the axial ribs, and four weaker cords, one above and three below shoulder. Penultimate whorl with 17 low axial ribs that gradually become indistinct, crossed by four shallow spiral grooves above periphery. On last whorl, axial sculpture consists mainly of incremental scars, some of which are quite strong, and a few low and indistinct axial swellings; five shallow spiral grooves on the shoulder, periphery almost smooth, base with deeper grooves, six above labral notch, 12 below it, delimiting sharp spiral cords near siphonal canal. Incremental scars of labral spine shallow, distinct on part of the whorl, indistinct and merging with spiral grooves on part of the whorl. Aperture ovoid, elongate, comprising 43% of total shell height. Outer lip thin (not adult), without projecting labral spine. Siphonal canal broad, very short. Inner lip with thin glossy callus. Columella with three plaits, adapical one stronger.

Color: protoconch light yellowish tan; first three teleoconch whorls whitish, subsequent whorls gradually darkening to light chestnut brown on penultimate and last whorls, with the exception of a narrow whitish subsutural band.

Dimensions: height 21.0 mm, diameter 9.5 mm, body whorl length 14.7 mm, aperture height 9.0 mm.

Remarks: The specimen from SMIB 8 sta. DW193–196 is an old and worn adult with a broken outer lip, height 38.0 mm. Its last adult whorl has no trace of axial sculpture, but there are five spiral grooves above the shoulder and 15 at the base of the shell, below a broad, distinct, and continuous band corresponding to scars of a probably short labral spine.

C. ***leios*** differs from all other species of *Ceratoxancus* by the absence of axial sculpture on subadult and adult whorls. Juveniles consistently have 11 distinctly shouldered axial ribs instead of 11–14 broader ribs in juveniles of *C. teramachii.*

Placement of *C. **leios*** in *Ceratoxancus* is justified by the general shell morphology which resembles that of *C. teramachii,* and the presence of a labral spine fasciole below periphery of the last adult whorl.

Etymology: From the Greek *leios,* meaning smooth, with reference to the absence of shell sculpture on adult whorls.

*Ceratoxancus **basileus*** Kantor & Bouchet, sp. nov.

(Figures 3A, B, 5, 7H–J)

Type material: Holotype in MNHN.

Type locality: SMIB 2: R/V *Vauban,* sta. DW18b, 22°58′S, 167°20′E, 530–535 m.

Material examined: NEW CALEDONIA. BIOCAL, R/V *Jean-Charcot,* sta. DW33, 23°10′S, 167°10′E, 675–680 m, 1 lv. MUSORSTOM 4: R/V *Vauban,* sta. DW221, 22°59′S, 167°37′E, 535–560 m, 4 dd. Sta. DW223, 22°57′S, 167°30′E, 545–560 m, 1 dd. SMIB 2: R/V *Vauban,* sta. DW18b, 22°58′S, 167°20′E, 530–535 m, 1 dd (holotype). SMIB 3: R/V *Vauban,* sta. DW21, 22°59′S, 167°19′E, 525 m, 1 dd. BATHUS 2: R/V *Alis,* sta. DW720, 22°52′S, 167°16′E, 530–541 m, 1 dd.

Distribution: New Caledonia, alive in 675–680 m, shells from 525 m.

Description: Shell ovoid, fusiform, solid, glossy, consisting of 1.2+ protoconch and eight slightly convex, nearly flat teleoconch whorls, with shallow impressed suture. Nucleus and initial part of protoconch II chipped, remaining part smooth, corroded, with protoconch/teleoconch transition indistinct, diameter ca. 950 μm. Sculpture consisting of strong orthocline ribs crossed by weaker spiral cords. There are 11–12 very distinct and strong ribs per whorl on first four whorls, more numerous on subsequent whorls, up to 19 on penultimate whorl. Last adult whorl almost smooth, with low, broad, and indistinct axial varices. Spiral sculpture poorly defined on all teleoconch whorls, except one strong cord at shoulder, forming a nodulous intersection with the axial ribs; four much weaker cords, one above and three below shoulder, distinct on early spiral whorls, obsolete on later whorls. In addition, there is a second-order sculpture consisting of fine incremental lines and fine spiral riblets. This sculpture is best seen in the depressions between main ribs and cords, and is especially distinct above the shoulder. On the last whorl, the only main sculpture present is the strong spiral cord at the shoulder, and the apparently smooth periphery is sculptured by fine spiral grooves and more indistinct incremental lines. There are 12 much stronger spiral cords toward the base of the whorl and on the siphonal canal. Aperture elongate, comprising 39% of total shell height. Siphonal canal rather broad, short. Inner lip with thin glossy callus (outer lip broken). Columella with three plaits, the adapical one stronger. Only two adapical plaits are seen in apertural view, the third one is seen only when the shell is turned clockwise ¼ of a whorl.

Color: protoconch very light yellowish tan; first three teleoconch whorls whitish, subsequent whorls gradually darkening to light chestnut brown, with the exception of a light violet band centered on shoulder cord; transition from violet to brown very gradual.

Dimensions: height 56.1 mm, diameter 19.5 mm, last whorl height 38.3 mm, aperture height 21.6 mm.

Remarks: The live-collected specimen from BIOCAL sta. DW33 has a rather thick, smooth periostracum tightly adhering to the shell surface. It is worn on the axial ribs.

*Ceratoxancus **basileus*** is similar to *C. **leios*** and differs by its larger adult size, taller spire, and longer siphonal canal, as well as the absence of a labral spine or fasciole. In *C. **basileus*** the axial sculpture is present in subadults 50 mm high and becomes obsolete only on the last whorl of large adults; in *C. **leios,*** sculpture is restricted to juvenile whorls.

Etymology: From the Greek *basileus:* king, because this is the largest of the known species of *Ceratoxancus.*

DISCUSSION

Comparative Remarks

Six species of *Ceratoxancus* are recognized as a result of the present work, and they can be easily discriminated by a suite of conchological and anatomical characters (Table 1). Only *C. elongatus* and *C. **melichrous*** have a fairly similar general appearance, and accurate identification of single shells requires that protoconch characters are available.

In forthcoming papers, we will report on the anatomy of *Latiromitra* Locard, 1897, and *Benthovoluta* Kuroda & Habe, 1950, and discuss the phylogeny and classification of Ptychatractinae and Turbinellidae. The present discussion is therefore preliminary and aims only at placing *Ceratoxancus* in a broader context. In his review of the subfamily Ptychatractinae, Harasewych (1987) assigned to it seven genera: *Ptychatractus* Stimpson, 1865, *Surculina* Dall, 1908, *Benthovoluta, Metzgeria* Norman, 1879, *Cyomesus* Quinn, 1981, *Latiromitra,* and *Ceratoxancus,* and expressed doubts about the taxonomic position of the latter two. *Ceratoxancus* shares a number of anatomical characters with *Latiromitra* and *Benthovoluta* (based on our own unpublished results): (1) a short or very short proboscis, (2) paired proboscis retractors, (3) the position of the buccal mass and opening of the radular diverticulum into the buccal cavity at the proboscis base in its contracted position, (4) the ventral odontophore retractor passing through the nerve ring, (5) the presence of a single accessory salivary gland, (6) a large gland of Leiblein, (7) mid-esophagus with well-developed dorsal glandular folds, and (8) a small stomach. Therefore we may conclude that *Benthovoluta, Latiromitra,* and *Ceratoxancus* constitute a

Table 1

Conchological and anatomical characters discriminating the species of *Ceratoxancus*. n.a.: data not available.

	teramachii	*elongatus*	*melichrous*	*niveus*	*leios*	*basileus*
Maximum adult size (mm)	31.5	32.2	20.4	8.8	38.0	56.1
Number of protoconch whorls	2.5	2.5	1.5	1.0	3+	n.a.
Labral fasciole	Present	Present	Absent	Absent	Present	Absent
Sculpture on last adult whorl	Axial ribs variable spiral cords	Axial ribs + spiral cords	Axial ribs + spiral cords	Axial ribs + spiral cords	Smooth	Smooth
Operculum length/aperture length	>0.4	0.12	0.5	0.45	n.a.	0.37
Radula width/aperture length (%)	1.17	1.58	2.86	1.76	n.a.	2.55
Mid-esophagus/proboscis length	5	5	2.5	n.a.	n.a.	6.5
Salivary glands	Not fused	Not fused	Fused	n.a.	n.a.	Not fused
Accessory salivary gland	Present	Present	Absent?	n.a.	n.a.	Present
Penial papilla	Present	Absent	Absent	Absent	n.a.	Present
Anterior part of gland of Leiblein	Coiled	Coiled	Not coiled	n.a.	n.a.	Coiled

group which, judging from the radular morphology, should include the genus *Ptychatractus* and thus belong to the subfamily Ptychatractinae.

Anatomy is rather uniform among the species of *Ceratoxancus*. A character that varies significantly within the genus is the length of the mid-esophagus. It is long and coiled in *C. teramachii* and *C. elongatus* (thus in both species possessing a labral spine) and shorter in *C. **melichrous***, which lacks a spine. Such differences may be connected with diet-specific feeding mechanisms. Reduction of operculum size has apparently occurred several times in the subfamily. Besides *C. elongatus*, where it is greatly reduced, a non-operculate species was found in *Latiromitra*, and in an unnamed species of *Benthovoluta*, the presence of the operculum seems to be intraspecifically variable (Bouchet & Kantor, unpublished observations).

There is also some variation in the radula of *Ceratoxancus* species. Two types of rachidian teeth can be recognized. In *C. teramachii* (Figure 2B), *C. **melichrous*** (Figure 2F), and to some extent also in *C. **niveus*** (Figure 3F), the rachidian teeth are rather long, with the cusps emanating closer to the posterior edge of the basal part. In *C. elongatus* (Figure 3D) and *C. **basileus*** (Figure 3B), the rachidian teeth are short with much shorter cusps, which emanate closer to the anterior edge of the basal part. There is no correlation between the form of the rachidian and lateral teeth. Thus, in *C. teramachii* the lateral teeth have a very long base (Figure 2C). Much shorter bases are found in *C. elongatus* and *C. **basileus***. Conversely, in *C. **melichrous*** and *C. **niveus***, the lateral teeth are very long, but their base is very short. This radular morphology is rather similar to that of other ptychatractines. The radula of *C. **melichrous*** resembles closely that of *Ptychatractus ligatus* (Harasewych, 1987: fig. 19), while radulae of *C. elongatus* and *C. **basileus*** are very similar to that of *Latiromitra chaunax* (Bayer, 1971) (Harasewych, 1987: fig. 20). This is in contrast to radular morphology in Vasinae and Turbinellinae, the former having a bicuspid rachidian tooth, while in the latter it is very broad with long lateral flaps (Harasewych, 1987: figs. 21, 22). In Columbariinae, the rachidian teeth are similar in shape to those of Ptychatractinae, but differ in having a deeply arched base (Harasewych, 1983: figs. 9–12).

Mode of Development

The protoconchs of *C. **melichrous*** and *C. **niveus*** are both paucispiral and indicate non-planktotrophic development. However, the protoconch of *C. **melichrous*** has a small initial nucleus, it has 1.5 whorls with a distinct protoconch/teleoconch transition, and its color is light yellowish brown: this indicates most probably a lecithotrophic development, possibly with a short, free-swimming demersal phase. By contrast, the protoconch of *C. **niveus*** has a large initial nucleus and it has only one whorl with an indistinct transition to the teleoconch: this most probably indicates a development with intracapsular metamorphosis. The protoconchs of the other four species, *C. teramachii*, *C. elongatus*, *C. **basileus***, and *C. **leios***, are multispiral and indicate planktotrophic larval development.

The broad distribution of *C. teramachii* and *C. elongatus* is probably correlated with the good dispersal capacities of planktotrophic larvae and, based on their protoconch morphology, it is likely that *C. **leios*** and *C. **basileus*** will also be discovered in other parts of the Indo-West Pacific.

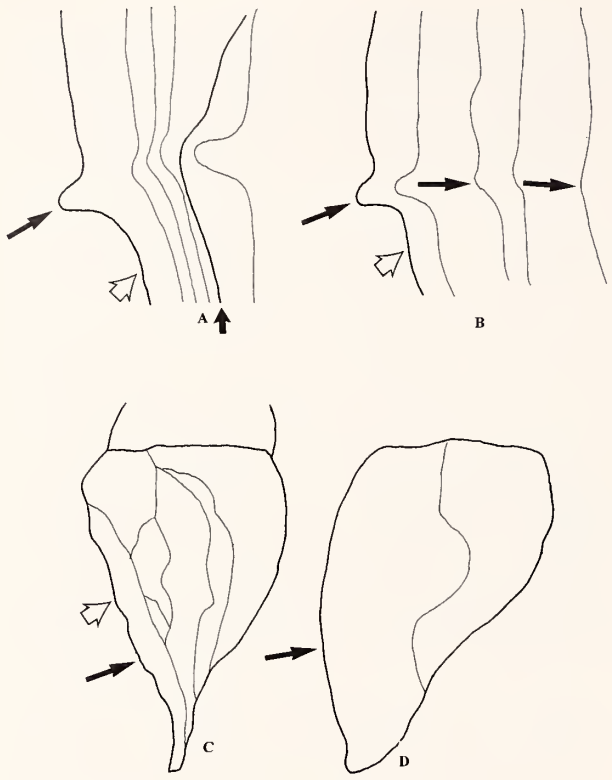

Figure 8

Ceratoxancus elongatus (A–B). A, shape of the incremental lines on the last teleoconch whorl, showing reappearance and progressive development of the labral spine after aperture lip breakage; B, shape of the incremental lines, showing variation of the labral spine length without aperture lip breakage. *Ceratoxancus teramachii* (C, D). C, last teleoconch whorl of the specimen with numerous scars of form A; D, last teleoconch whorl of the specimen with scar of form B. Large hollow arrows indicate aperture lip. Long filled arrows indicate the labral spine, or its position when the spine is not pronounced. Short filled arrow indicates the scar from shell breakage.

By contrast, *C.* ***melichrous*** and especially *C.* ***niveus*** may have a distribution restricted to the Norfolk Ridge, correlated with the poor dispersal capacities of their larvae.

What is the Function of the Labral Spine?

A remarkable feature of three species of *Ceratoxancus, C. teramachii, C. elongatus,* and probably *C.* ***leios,*** is the presence of a labral spine. The degree of spine development greatly varies from specimen to specimen, as well as during the lifetime of an individual. This is revealed by the shape of growth lines on the last teleoconch whorl. On the upper whorls, the spine fasciole is covered by successive whorls.

In *C. teramachii* and *C. elongatus,* there are numerous scars from breakages of the apertural lip (see below). As a rule, and as one would expect, immediately after the apertural breakage the spine is either absent or very short (Figure 8A). In *C. teramachii,* over time it becomes longer until the next breakage. In *C. elongatus,* breakages are less frequent, and therefore, a longer part of the undamaged body whorl can be examined, revealing that the length of the spine may change even without visible signs of damage (Figure 8B). The limited material of *C.* ***leios*** does not allow an estimation of the variability of prominence of the spine. In the holotype, the growth lines on much of the last teleoconch whorl are only slightly bent at the position expected for the spine, suggesting that a spine was present, although short and blunt. Conversely, in the largest specimen (SMIB 8, sta. DW193–196), the spine was probably present on the whole length of the last teleoconch whorl.

All studied specimens of *C. teramachii* have scars from numerous breakages of the apertural lip (Table 2), starting on the very first teleoconch whorls. Their number ranges from 0.14 to 2.43 per teleoconch whorl, and specimens collected off New Caledonia have more numerous scars (mean = 1.81, σ = 0.45) than those from the Coral Sea (mean = 0.36, σ = 0.28). There are two forms of scars. The more numerous breakages are prosocline and affect the area of the labral spine (form A) (Figure 8C). Much fewer are shallow or moderately deep notches on the periphery of the whorl that do not affect the area of the labral spine (form B) (Figure 8D). In *C. elongatus,* there are also traces of numerous breakages of the apertural lip (Table 3), varying in number from 0.25 to 1.37 per teleoconch whorl (mean = 0.72, σ = 0.37), which is fewer than in *C. teramachii.* As in the case with the latter species, the scars were of both types, and type B scars were also less numerous. The number of shell breakages in *C.* ***melichrous*** and *C.* ***basileus*** was yet smaller (Tables 4, 5). One specimen of *C.* ***basileus*** presents a rather deep incision, about ⅓ of a whorl, rather narrow and occurring in the lower part of the last whorl at the border of the canal. In all other specimens of *C.* ***basileus,*** the breakages were present only on the last whorls.

These numerous shell repairs may indicate unsuccessful attacks of predators such as crabs or may be connected with usage of the outer lip and labral spine for prey capture. In the latter case, the lip may be broken, e.g., during opening of valves of large bivalve mollusks. In shallow water, predatory crabs usually produce deep cuts in the shell to reach the body (Vermeij, 1993). Very similar scars were found in several specimens of *Benthovoluta claydoni* and *B.* sp., collected off New Caledonia. The length of such incisions may reach half of a whorl without killing the mollusk. Type B scars in *C. teramachii* have some similarity to crab predation scars, although they are much shallower. Thus one can suppose that the scars of this type may represent unsuccessful attacks on the snails. In an attempt to evaluate the connection of shell damage to crab predation, we counted the number of breakages on the shells of two forms of *Cantharus*-like buccinids from New Caledonia with similar shell thickness, shape, and from the same localities and depth range (415–600 m). The

Table 2

Number of apertural damages in *Ceratoxancus teramachii* in relation to size and locality. (Only the major breaks were considered).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl	Source
30.0 (incomplete)	8	11	1.38	S New Caledonia
25.7 (incomplete)	7	17	2.43	S New Caledonia
22.4 (incomplete)	5	9	1.80	S New Caledonia
26.4 (incomplete)	5	9	1.80	New Caledonia
21.2	6.5	9	1.38	S New Caledonia
30.0	7.5	11	1.47	S New Caledonia
26.2 (incomplete)	5	12	2.40	S New Caledonia
			mean = 1.81	σ = 0.45
16.0	5.5	1	0.18	Coral Sea
18.3	6	5	0.83	Coral Sea
21.7	7	1	0.14	Coral Sea
15.0	5.5	2	0.36	Coral Sea
28.8	7.5	2	0.28	Coral Sea
			mean = 0.36	σ = 0.28

number of breakages per teleoconch whorl was significantly lower than in both species of *Ceratoxancus* with spine: mean values for these buccinids were 0.19 (σ = 0.17, n = 13) and 0.40 (σ = 0.36, n = 11). The number of breakages per whorl in the latter species of *Cantharus* is extremely close to that in *C.* ***melichrous***. Moreover, type B scars are more numerous than those of type A.

As it is difficult to suppose that different species of *Ceratoxancus* have selectively different attractiveness to predators, the numerous shell breakages may not be connected with predation by crabs. The labral spine in *C. elongatus* is much less developed than in *C. teramachii,* and totally absent in *C.* ***melichrous*** and *C.* ***basileus***. Thus, the number of breakages in different *Ceratoxancus* spp. increases with the degree of development of the spine. Therefore, it seems likely that the apertural lip and particularly the spine are used for prey capture.

Nothing is known about feeding and diet of any species of the genus possessing a spine. The digestive tract in studied specimens did not contain any recognizable food particles. The only dissected specimen of *C.* ***melichrous*** had presumably sponge spicules and parts of minute crustaceans in the stomach and rectum. We can also suppose that *C.* ***basileus*** either drills, or rasps some prey with a very hard skeleton. This is indirectly suggested by the

Table 3

Number of apertural damages in *Ceratoxancus elongatus* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
20.4	6	6	1.00
18.0	5	1	0.25
18.7	5	4	1.25
17.5	5.2	2	0.38
15.5	5	3	0.75
16.4	5	5	1.00
19.2	5.4	2	0.37
19.5	5.5	3	0.55
22.1 (incomplete)	5.2	6	1.15
24.2	5.8	8	1.37
18.6	5	3	0.6
20.6	5.3	2	0.37
20.3	5.5	4	0.73
29.5 (incomplete)	6.2	6	0.98
20.1	5.5	2	0.36
		mean = 0.72	σ = 0.37

Table 4

Number of apertural damages in *Ceratoxancus melichrous* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
20.4	7	2	0.29
18.0	6.7	1	0.15
14.0 (incomplete)	4	4	1.00
15.2 (incomplete)	4	2	0.5
17.5	6	2	0.33
16.4	6.5	0	0.00
		mean = 0.38	σ = 0.35

Table 5

Number of apertural damages in *C. basileus* in relation to size (all from New Caledonia).

Shell length (mm)	No. of teleoconch whorls	No. of apertural scars	Scars per whorl
56.1	7.7	1	0.13
56.5 (incomplete)	8.0	3	0.38
54.2 (incomplete)	7.5	2	0.27
45.6 (incomplete)	7.5	3	0.4
43.5	7.5	2	0.27
49.7	8.5	1	0.12
50.0 (incomplete)	6.5	1	0.15
		mean = 0.25	σ = 0.12

extremely worn teeth on the bending plane of the radula (Figure 3B). This was not observed in spined species. Bivalves or barnacles may represent potential prey for the spined species of *Ceratoxancus*. Examination of the overall faunal composition at some stations that yielded *Ceratoxancus* revealed that no large bivalves with thick shell are present. Also, the barnacles present were easily opened with the fingernail, and it is hard to imagine how they could induce shell breakage on a potential predator. Thus the prey of *Ceratoxancus* remains unknown. The significant differences in the number of apertural breakages between populations of *C. teramachii* from New Caledonia and the Coral Sea may be connected with local differences in feeding regimes.

Note Added in Proof:

While the present paper was in press, new expedition material has been processed in MNHN. It contains new records of *Ceratoxancus* from Vanuatu and the Economic Zone of Wallis & Futuna (a French dependant territory NE of Fiji).

Ceratoxancus teramachii:
SW PACIFIC. MUSORSTOM 7: R/V *Alis*. **WATERWITCH BANK**. Sta. DW537, 12°30′S, 176°41′W, 325–400 m, 1 dd. Sta. DW573, 12°31′S, 176°52′W, 364 m, 1 lv.
COMBE BANK. Sta. DW542, 12°26′S, 177°28′W, 370 m, 1 lv.

Ceratoxancus elongatus:
SW PACIFIC. MUSORSTOM 7: R/V *Alis*. **WATERWITCH BANK**. Sta. DW575, 12°31′S, 176°52′W, 425 m, 1 dd.
Sta. DW636, 13°39′S, 179°55′E, 650–700 m, 1 dd.

Ceratoxancus ***melichrous***:
VANUATU. MUSORSTOM 8: R/V *Alis*, sta. DW978, 19°23′S, 169°27′E, 408–413 m, 1 lv.

Ceratoxancus ***leios***:
SW PACIFIC. MUSORSTOM 7: R/V *Alis*. **TUSCARORA BANK**. Sta. CP562, 11°48′S, 178°22′W, 775–777 m, 1 dd.
Sta. DW635, 13°49′S, 179°56′E, 700–715 m, 1 dd.

The new material confirms our supposition that *C.* ***leios*** has a broader SW Pacific distribution. It also confirms that *C.* ***melichrous*** probably has a short free-swimming demersal phase but, contrary to our supposition, it is not a Norfolk Ridge endemic.

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